

Oviposition, host plant choice and survival of a grass feeding butterfly, the Woodland Brown (*Lopinga achine*) (Nymphalidae: Satyrinae)

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Abstract. Oviposition, host plant choice and survival on different plants of a grass-feeding butterfly, *Lopinga achine*, were studied in the field and in the laboratory. Grass-feeding butterflies are generally thought to be non-specific in their host plant choice. This seems not to be true for *L. achine*. Females were selective in their host plant choice and preferred to oviposit near *Carex montana*, although they do not attach their eggs to any plant. *Carex montana* was also generally preferred by the larvae in laboratory experiments among the plants available in the field. However, the larvae preferred three species that they seldom encounter in the field (*Agrostis capillaris*, *Phleum pratense* and *Poa pratensis*) before *C. montana* when they were offered these four species. Most of the larvae found in the field (>80%), were found on *C. montana*. The larvae survived significantly better on *C. montana* than on six other species in rearing experiments. The results indicate that host plant choice occurs in two steps in *L. achine*: 1) the females choose a patch to drop the egg to the ground, usually in the vicinity of a *C. montana* plant 2) the newly hatched larva moves to the host plant. The apparent dependence of the Swedish mainland *L. achine* population on a single host plant has important conservation implications.

KEY WORDS: *Lopinga achine*, Satyrinae, host plant choice, performance, larvae, conservation, *Carex montana*.

INTRODUCTION

Lopinga achine Scopoli (Nymphalidae: Satyrinae) is one of the threatened Swedish butterflies that may disappear from the Swedish mainland without conservation measures. The species is classified as endangered in three European countries and as vulnerable in four (Heath 1981). It is one of the few Swedish species on the Bern Convention list (Council of Europe 1993) of endangered flora and fauna in Europe. The species is local throughout its distribution area from the south of Fennoscandia through central Europe to North and Central Asia and Japan (Kudrna 1986). In Sweden it lives in two areas, in the province of Östergötland, where I am studying it, and on the island of Gotland in the Baltic (Henriksen & Kreutzer 1982).

Little is known about the host plant of *L. achine*. The female drops the eggs to the ground and does not attach them to plants. Consequently it is difficult to ascertain its host plants (Karlsson & Wiklund 1985). At least 15 species or genera within Poaceae and Cyperaceae are suggested as host plants in the literature (Nordström 1955, Henriksen & Kreutzer 1982; Karlsson & Wiklund

1985; Ackery 1988; Lepidopterologen-Arbeitsgruppe 1988; Jutzeler 1990;). Only three of the plants seem to be confirmed by larval findings in the field. One larva was found on *Carex alba* Scop. and one on *C. montana* L. (Cyperaceae) (Ebert & Rennwald 1991) and larvae (numbers not stated) were also found on *Brachypodium sylvaticum* (Huds.) PB (Poaceae) (Lepidopterologen-Arbeitsgruppe 1988).

Knowledge about host plants is still poor in many butterfly species, especially in grass-feeding ones (Thomas 1984). Grass feeding butterflies are generally thought to be unspecific in their choice of oviposition site (Wiklund 1984), but the studies of this are few in number. Our present knowledge of host-plant choice and oviposition in butterflies is based primarily on studies of Pieridae, Heliconiidae, *Papilio* spp. and *Euphydryas* spp. (e.g. Thompson & Pellmyr 1991, Renwick & Chew 1994). Many butterfly species have been shown to be more specific in their choice of habitat in the young stages than first had been suspected. Therefore it is necessary to know the exact needs of the immature stages to make conservation successful (Thomas 1984, Thomas 1991, New et al. 1995).

The aim of this investigation is to study the host plant choice of *Lopinga achine* and to determine its degree of specificity.

MATERIALS AND METHODS

Study animal and study site

L. achine fly in one generation in June-July and hibernates in the larval stage. The typical habitat in Östergötland, where I study it, is partly open oak woodland (*Quercus robur* L.) (Fagaceae) with hazel (*Corylus avellana* L.) (Corylaceae). This habitat is a successional stage lasting 30-50 years before the canopy closes if not grazed. The habitat on Gotland is different, being partly open coniferous forest with a well-developed scrub layer of *Frangula alnus* Mill. (Rhamnaceae), *Sorbus aucuparia* L. (Rosaceae), *S. intermedia* (Ehrh.) Pers. and *Juniperus communis* L. (Cupressaceae). According to inventories up to 1997, *L. achine* lives in 49 populations in Östergötland in a small area (21 x 10 km) and most of the populations have contact with each other according to mark-recapture work. The matrix is usually open fields or spruce plantations. Most populations are small, some hundreds of adults. Four populations may comprise two to three thousand adults.

Oviposition

Ovipositing females were followed in the field in areas of high adult density. I used binoculars to be able to observe the females from a distance in order not to disturb them. Immediately after oviposition the exact place was marked and all Poaceae, Juncaceae and Cyperaceae species within 15 cm were recorded. Plant names follow Mossberg (1992). All females I saw ovipositing did so sitting on the vegetation. The oviposition place is henceforth referred to as an "oviposition point". The observations were mainly (48 out of 84 egg-layings) made in the largest population and the rest in nine other populations.

Plant species at randomly selected points were checked in the same manner as the oviposition points. These "random points" were placed at approximately the same distance from the edge (one meter zones) between forest and open areas as the oviposition points to avoid vegetation differences due to influence from the forest.

For example, a oviposition point 1.7 meters from the edge of the glade in the forest has a corresponding random point between 1-2 meter from the edge.

Larval host-plant choice in the laboratory

The larval host-plant choice was tested in the laboratory using different grasses and sedges (Table 1.) during the season when larvae normally feed. The laboratory temperature varied between 22° and 25°C and there was limited daylight (50-80 lux) from a small window above the petri dishes. Plant leaves were cut in 25 mm long pieces and placed in a circle with the cut ends towards the centre of a petri dish (9 cm diameter). Each plant species was represented by one piece, except the thin *Deschampsia flexuosa* (L.) Trin. (Poaceae) with several pieces in each place. Moist filter paper covered the bottom in the dish. The leaves rested against a roll of paper at the edge of the dish to prevent them from laying flat on the bottom. During all the trials, only two larvae made no choice.

Eggs were collected from 20 females caught in the wild and kept together in a cage. All of them laid eggs and the collected eggs was a mixture from these 20 females. A newly hatched larva arising from each of these eggs was placed in the middle of each petri dish with a fine brush. After 72 hours, the plant species were ranked according to larval preferences: plants with the largest area eaten of was ranked as number one, that with the second largest area eaten as number two and so on to the last one.

Host plant choice in the field

In the glades where I had found the largest numbers of flying adults, I systematically searched through every plant in the families Poaceae, Juncaceae and Cyperaceae for larvae in a zone six meters out in the open glade and six meters under the tree and bush cover. I noted the species upon which they were found. This was done in four populations in the autumn (20.IX.90-3.X.90) and spring (22.V.91-6.VI.91).

Rearing experiments on different plant species

In 1989-90 I reared larvae on five putative hostplants: *Calamagrostis arundinacea*, *Carex montana*, *Deschampsia cespitosa*, *Melica nutans* and *Poa nemoralis*. The larvae originated from the eggs from the captured females mentioned earlier. The larvae were reared outdoors in 18 x 18 x 18 cm cages with net sides. Each cage contained 10 larvae and the plants stood in water. The plants were changed every third day for the first two weeks, and then weekly or when deteriorated. The cages were moved into the laboratory in November and kept at 4°C until March. In February, the larvae were offered pieces of the plants that had green shoots in the field. Survival and weight (0.1 mg) were followed up to and including adult eclosion. Pupae were not weighed in order not to disturb them so the last weighing before weighing the adults was of mature larvae. The newly hatched larvae were too small to be weighed individually so 57 were weighed together and the average was used as a starting weight. Adults were weighed one day after eclosion.

In the second experiment (1991-92), the larvae were reared in round plastic cages 10 cm high and 11 cm in diameter, with a net lid. The larvae came from 20 females caught in the wild and kept individually and the offspring were mixed as evenly as possible. Five larvae were reared in each cage. The plants roots were submerged in water through a hole in the bottom of each cage. The plants were changed whenever they showed signs of deterioration. Seven plants (Poaceae and Cyperaceae) were tested: *Agrostis capillaris* L., *Calamagrostis arundinacea*, *Carex montana*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Milium effusum* L., *Phleum pratense* L. Survival was followed up to

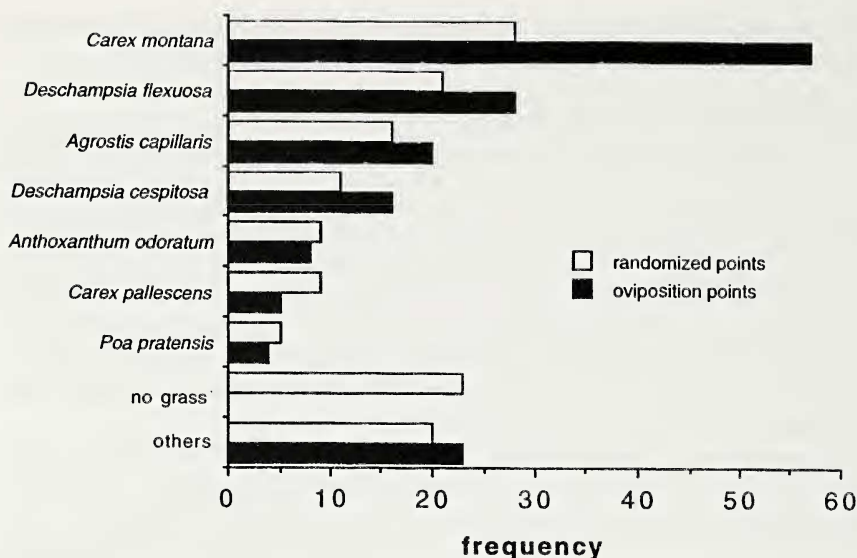


Fig. 1. Grass and sedge species within 15 cm from oviposition points of *Lopinga achine* and within 15 cm from randomly selected points ($n=84$ in both cases). Plant species with less than five occurrences among the randomly selected points are pooled as "others." These species are also grouped as "others" at the oviposition points.

and including adult eclosion. The entire experiment including hibernation was conducted outdoors.

Statistics

All statistics were calculated using Statview 4.01 for Macintosh (Haycock et al. 1992).

RESULTS

Oviposition

The plant frequency in the randomly chosen points was significantly different from the frequency in the oviposition points ($\chi^2=35.7$; $p<0.0001$; $df=8$) (Fig. 1). Females preferred to oviposit near *Carex montana*. No female oviposited at points lacking grasses or sedges although 23 of the 84 randomly selected points lacked grasses and sedges. Therefore I excluded these 23 points and tested whether the frequency of *C. montana* differed between oviposition points and the 61 randomly selected points with grasses and sedges. The difference is significant ($\chi^2=7.0$, $p<0.01$, $df=1$), 57 out of 84 females (68%) oviposited within 15 cm from *C. montana*, but it occurred at only 28 of the 61 randomly selected points (46%) with grasses and sedges.

Larval host plant choice

The newly hatched larvae clearly preferred some plants to others in all seven experiments (Table 1). *Carex montana* was preferred in four of five trials

where it occurred. However, *A. capillaris*, *Phleum pratense* and *Poa pratensis* were preferred to *C. montana* in one trial. Other preferred species were *M. nutans* and *P. annua*. *Deschampsia flexuosa* and *D. cespitosa* were generally disliked. The larvae refused to eat *D. flexuosa* completely.

Field observations of 97 larvae in the autumn confirmed the results of the larval host plant choice experiments. *Carex montana* was used by 82 larvae (85%), and nine were found on the low preferred host, *D. cespitosa*. One larva were found on each of *P. pratensis*, *Festuca rubra* L. (Poaceae), *Luzula pilosa* (L.) Willd (Juncaceae) and an unidentified Poaceae. Two were found on non-host material. The difference between *C. montana* frequency in ovipositions (57 of 84) and larval occurrence (82 of 97) is significant ($\chi^2=7.0$, $p=0.008$, $df=1$).

The result was almost the same in the spring. *C. montana* was used by 71 larvae of 86 (83%), and 10 used *D. cespitosa*. The other larvae were found on non-host material or when pupating.

Rearing experiments

The larvae grew slowly until hibernation started in October in the third instar (Fig. 2a). They grew fast in spring (March-June) to the fourth (most of the males) or fifth instar (most of the females) and pupation. The larvae were left undisturbed and eating for a week before they were weighed in the spring which is the reason for the apparent weight gain during hibernation. Adult weights among females reared on different plant species differ significantly ($p=0.007$, $F=4.68$; $df_1=4$, $df_2=21$, single-factor ANOVA). However, it is only the groups reared on *C. montana* and *D. cespitosa* that differ in a *post hoc* test ($p=0.017$, Scheffé's F). Male groups do not differ significantly from each other ($p=0.62$, $F=0.665$, $df_1=4$, $df_2=34$, single-factor ANOVA) (Fig. 2a).

There are significant differences in survival in the first experiment between larval groups feeding on *C. montana* and those feeding on *D. cespitosa*, *M. nutans* and *P. nemoralis* (χ^2 , $p<0.02$ three pairwise comparisons, $df=1$ in each comparison) but not between *C. montana* and *C. arundinacea* ($\chi^2=2.92$, $p=0.09$, $df=1$) (Fig. 2b). Larval mortality was highest during the first 50 days (July-August) and after hibernation. In the second rearing experiment, the survival on *C. montana* was significantly higher than on all the other species (χ^2 , $p<0.02$ six pairwise comparisons, $df=1$ in each comparison) (Fig. 3). The survival on *D. cespitosa* and *C. arundinacea* was low compared to the results in the first rearing experiment. There is also a tendency for increased mortality during the first days of this trial and again after hibernation but it is not as clear as in the first trial.

Mean time to eclosion for males varied between 334 days (*P. nemoralis*) and 338 days (*M. nutans*) (Fig. 4). Mean time to eclosion for females varied between 341 days on *D. cespitosa* and 348 days on *C. montana*. There are significant differences between times to eclosion between females ($p=0.006$, $F=4.93$, $df_1=4$, $df_2=21$, single-factor ANOVA) but not for males ($p=0.154$, $F=1.79$, $df_1=4$, $df_2=34$, single-factor ANOVA).

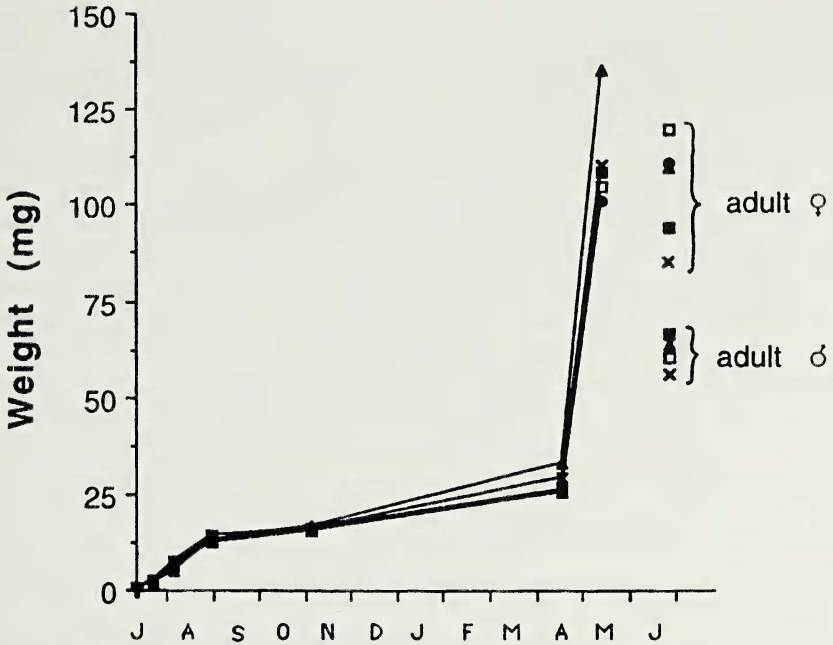


Figure 2a. Mean weight increase of *Lopinga achine* larvae and mean of adult weights at eclosion after development on five different grass species. Measures of spread are omitted for clarity. The largest SEs are $\pm 15,5\%$ for larvae and $\pm 10,9\%$ for adults. See Figure 2b number of larvae.

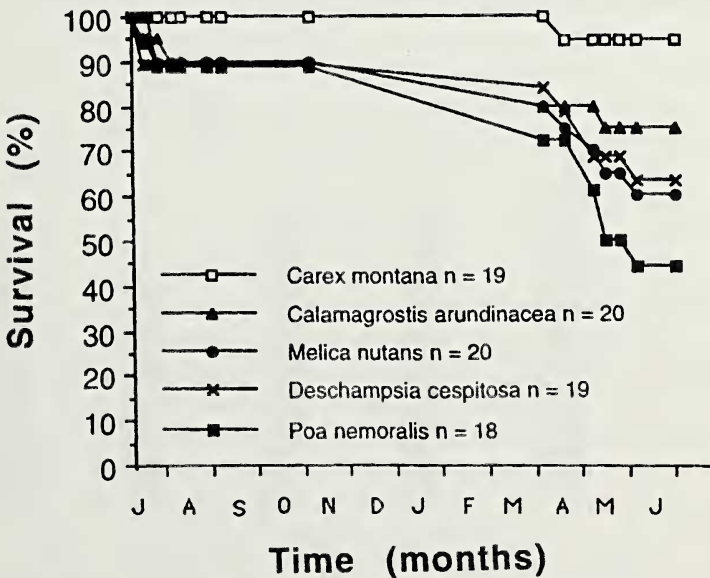


Figure 2b. Survival of *Lopinga achine* larvae to adult butterflies on five different plant species. The experiment was done 1989-1990 and started 8.VII outdoors but hibernation took place in the laboratory November-March. n = number of larvae.

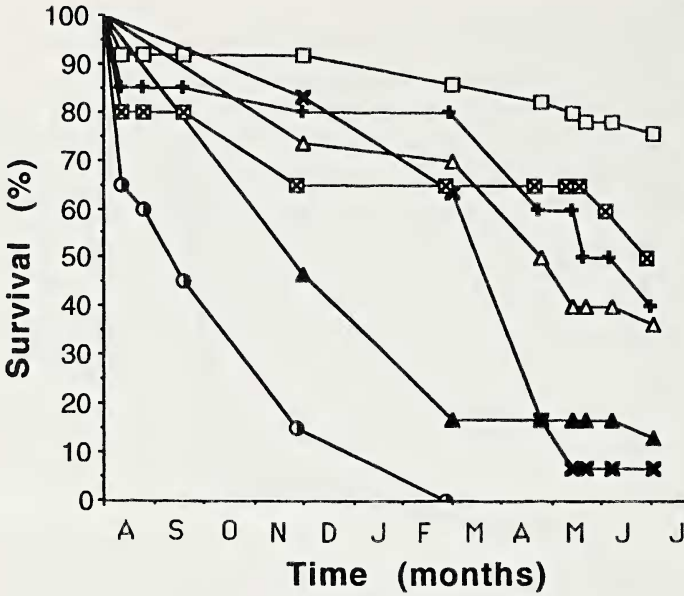


Figure 3. Survival of *Lopinga achine* larvae to adult butterflies on seven plant species. The experiment was done outdoors and started 4.VIII.1991. Plant species in decreasing order of butterfly survival: *Carex montana* (n=50), *Phleum pratense* (n=20), *Agrostis capillaris* (n=20), *Dactylis glomerata* (n=30), *Calamagrostis arundinacea* (n=30), *Deschampsia cespitosa* (n=30), *Milium effusum* (n=20). n = number of larvae reared.

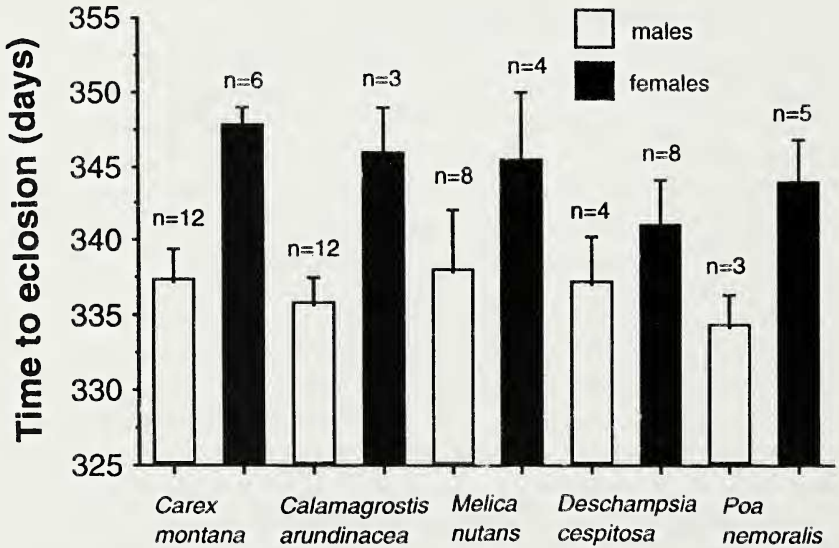


Figure 4. Mean development time to eclosion (\pm S.E.) of *Lopinga achine* males and females on five grass species. n = number of butterfly specimens.

DISCUSSION

It is clear that *L. achine* females prefer to oviposit near *C. montana* (Fig. 1), even though they do not attach their eggs to that plant. This selective oviposition behaviour contrasts to the suggestions of Wiklund (1984) that the satyrines that do not attach their eggs do not bother much about where they drop them. Polyphagy or superabundant host plants are suggested as reasons for the behaviour (Wiklund 1984, Thompson & Pellmyr 1991). Neither seems to be true for *L. achine* populations in Östergötland when looking at the selective host plant choice and the difference in survival on different plants. It is important to note that *C. montana* is not superabundant in large areas of the *L. achine* sites even though the species was the most common grass species in the areas where the females oviposited. This indicates that the females first make a habitat choice. After the habitat choice, the host plant choice seems to occur in two steps in *L. achine*: 1) the females choose a patch to drop the egg to the ground 2) the newly hatched larvae move to the host plant (only tested under laboratory conditions).

Lopinga achine females show the characteristic fluttering flight before landing and oviposition (Porter 1992). This indicates that the female does not drop the egg without regard to the environment. During this flight the females may use shapes (Vaidya 1969, Stanton 1982), colour (Saxena & Goyal 1978) and odour (Petersen 1954, Feeny et al. 1989) to locate host plants. Wing fluttering increased in *Papilio polyxenes* in the presence of host plant odours (Feeny et al. 1989). Many species also use contact stimuli (Chew & Robbins (1984) and references therein) before they oviposit. This does not seem to be the case in *L. achine* females as they sometimes oviposited in a tussock of *C. montana* when sitting on other plants growing together with *C. montana*, for example *Lathyrus linifolius* (Reichard) Bässler (Fabaceae). The search for ovipositing places may also involve microclimatic conditions (Thomas et al. 1986, Petersen 1954) and levels of shade (Greatorex-Davies et al. 1993).

In many species it is the female who selects host plant by her oviposition. The newly hatched larvae cannot exercise host-plant preference in many species, as they lack sufficient powers of movement to leave the plant on which the eggs were laid (Singer 1971, Saxena & Goyal 1978, Ohsaki 1979, Singer et al. 1994). However, the larva of *L. achine* must make the final choice itself since the female drops the egg to the ground, although near a host plant. The larva is quite able to choose (Table 1zx). It is also able to starve longer than the newly hatched larva of *Papilio machaon* whose female glues the egg to the host plant (Karlsson & Wiklund 1985). They stated that the ability of the *L. achine* larvae to endure starvation may be regarded as an adaptation to the female's way of oviposition.

However, the plant species they can choose among are determined by the egg-laying females (Fig. 1). That is probably one reason why larvae mostly occur on *C. montana*, even though they preferred *A. capillaris*, *P. pratense* and *P. pratensis* to *C. montana* in the experiments where all four species were

offered (Table 1). The larvae seldom encounter the three grasses in the field except for *A. capillaris* (Fig. 1), but this grass was often represented by just one or two leaves in the vicinity of the egg. Another reason for the significantly higher larval occurrence on *C. montana* (83-85%) in the field compared to ovipositions (68%), may be due to lower mortality of larvae on *C. montana* compared to other species. The larva may also be able to move longer than 15 cm, the distance arbitrarily chosen when checking plant species at oviposition points. About 10% of the larvae found in the field occurred on *D. cespitosa* but the larvae rated this species low in the choice experiments (Table 1). In the second rearing experiment it also caused high mortality (Fig. 3). However, it relatively often occurred at the oviposition points (Fig. 1). Its tussocks are large so it may be difficult to leave it if the egg hatches in the tussock. The development to adult may succeed on it (Fig. 2b, 4).

The developmental time does not seem to be important for host-plant choice in *L. achine*. The females on the preferred species, *C. montana*, had the longest time to adulthood (Fig. 4). Development time can be important if the time available for larval growth is limited (Nylin 1988).

Summarising, *L. achine* larvae survived and succeeded best on *C. montana*, and the plant species was also preferred by egg-laying females and newly hatched larvae in choice experiment among the plants available in the field (Table 1, Fig. 1, 2a,b, 3). The good correspondence between oviposition and performance in *L. achine* indicate that the generalist behaviour suggested for satyrids (Bink 1985) does not seem to be true for *L. achine*. The correlation between oviposition preference and performance in phytophagous insects varies much. Many studies have reported a good correspondence (e.g. Papaj & Rausher 1987, Nylin & Janz 1993) but many have also reported low correlations (e.g. Courtney 1981, Rausher 1979, Larsson & Strong 1992).

Carex montana is probably also the host plant for *L. achine* populations on the island of Gotland. *Carex montana* is very common in the woods that are habitat for *L. achine* there. *Lopinga achine* larvae from Gotland survived better on *C. montana* than on *D. glomerata* why Karlsson & Wiklund (1985) suggested *C. montana* as the major host plant. However, *C. montana* cannot be the single host plant for *L. achine* since the populations in Finland occur in areas without it (Hultén & Fries 1986). *L. achine* also completed the life cycle on many of the other plant species in my experiments, even though the success rate was lower. Different populations of butterflies may evolve different host plant preferences as in the satyrid *Satyrodes eurydice* Johansson (Shapiro 1974) and the nymphalid *Euphydryas editha* Boisduval (Singer et al. 1994), especially when living in different habitats.

The dependence of at least the Swedish mainland *L. achine* populations, on a single host plant has important conservation implications. In the future, the relations between the butterfly and the host plant may be studied to understand the reasons for the geographic distribution and to determine if there is a need for habitat management to ensure long-term survival.

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